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# The songs of the Palaearctic bush crickets of the tribe Drymadusini (Orthoptera: Tettigoniidae)

# Акустические сигналы кузнечиков трибы Drymadusini (Orthoptera: Tettigoniidae) Палеарктики

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КЛЮЧЕВЫЕ СЛОВА. Tettigoniidae, Drymadusini, звуковые сигналы.

ABSTRACT. Temporal pattern and frequency spectra of 13 species of palaearctic bush crickets of the tribe Drymadusini are given. Probable ways of calling song evolution in this tribe are discussed.

РЕЗЮМЕ: Приводятся данные об амплитудно-временных и частотных характеристиках звуковых сигналов 13 палеарктических видов кузнечиков трибы Drymadusini. Обсуждаются возможные пути эволюции их призывных сигналов.

Tribe Drymadusini includes at least 20 genera and 90 species of bush crickets from subfamily Tettigoniinae. Most of them spread in Central Asia and Near East. Only 11 species are known in Europe. As a rule they occure in the mountains where live on the stony slopes and screes. Until now acoustical signals of only 5 palaearctic species have been described [Dubrovin, Zhantiev, 1970; Zhantiev, 1981; Heller, 1988]. The results of recording and analysis of calling signals of 13 species from Crimea, Turkey, North Caucasus, Transcaucasia, Tuva and Far East are given here.

## Material and methods

Tape recordings were made in the laboratory and in the field.

Tape-recordings the songs of captive insects in the laboratory were made with use 1/4 inch Bruel&Kjaer 4135 or MK 301 RFT microphones with linear characteristics in the range 0.02-100 kHz, microphone ampliphier 2604 Bruel&Kjaer or 00 017 RFT and modified tape recorder "Yupiter-202 Stereo" with linear characteristic in the range 0.063–70 kHz. In this tape recorder the slowest standard tape speed of 9 cm/s was replaced by speed of 38 cm/s. Some earlier recordings were made without tape-recorder (direct connection of microphone amplifier with oscilloscope equipped by oscilloscopic camera FOR-2 with light sensitive film). Film speed (10 or 25 cm/s). gave opportunity obtain comprehensive registration of sound signals. Most of songs were stored on magnetic tape and than were digitazed (sampling rate 30.3; 58.8 or 142.8 kHz) and analyzed using the computer program TurboLab. All power spectra were obtained with linear amplitude scale.

All laboratory experiments were made in anechoic chamber in darkness at 20–26°C. Microphone without defensive grid was positioned at 8–10 cm of singing male.

In the field the cassette tape recorder with magnetic tape speed of 9 sm/s was used. It is impossible to make good recordings of high frequency katydid's sounds with such slow tape speed, and we used a bat detector QMC to transfere ultrasonic components in audible frequencies and record these new low frequency signals. Comparison of the oscillograms of sounds recorded in the field with bat detector and in the laboratory with high speed tape recorder has shown their high similarity in the temporal pattern. Of course frequency information in the first case was lost.

## Terminology

Rhythmic pattern of katydid's calling songs often is very complicated and difficult for description. Now many terms are used for designation of different components of the insect sound signals. For review see recently published excellent book of Ragge and Reynolds (1998). In our paper we have used following terms:
*pulse* (opening and closing) — sound produced by opening and closing wing-strokes at stridulation;
*series* (=echemes of Ragge, Reynolds, 1998) or *chirp* — the first order assemblage of pulses;
*series sequences* — the second order assemblages of pulses and the first order assemblages of series;
*phrase* — the second order sequence of series;
*trill* — continuous train of uniform pulses lasting indefinitely.

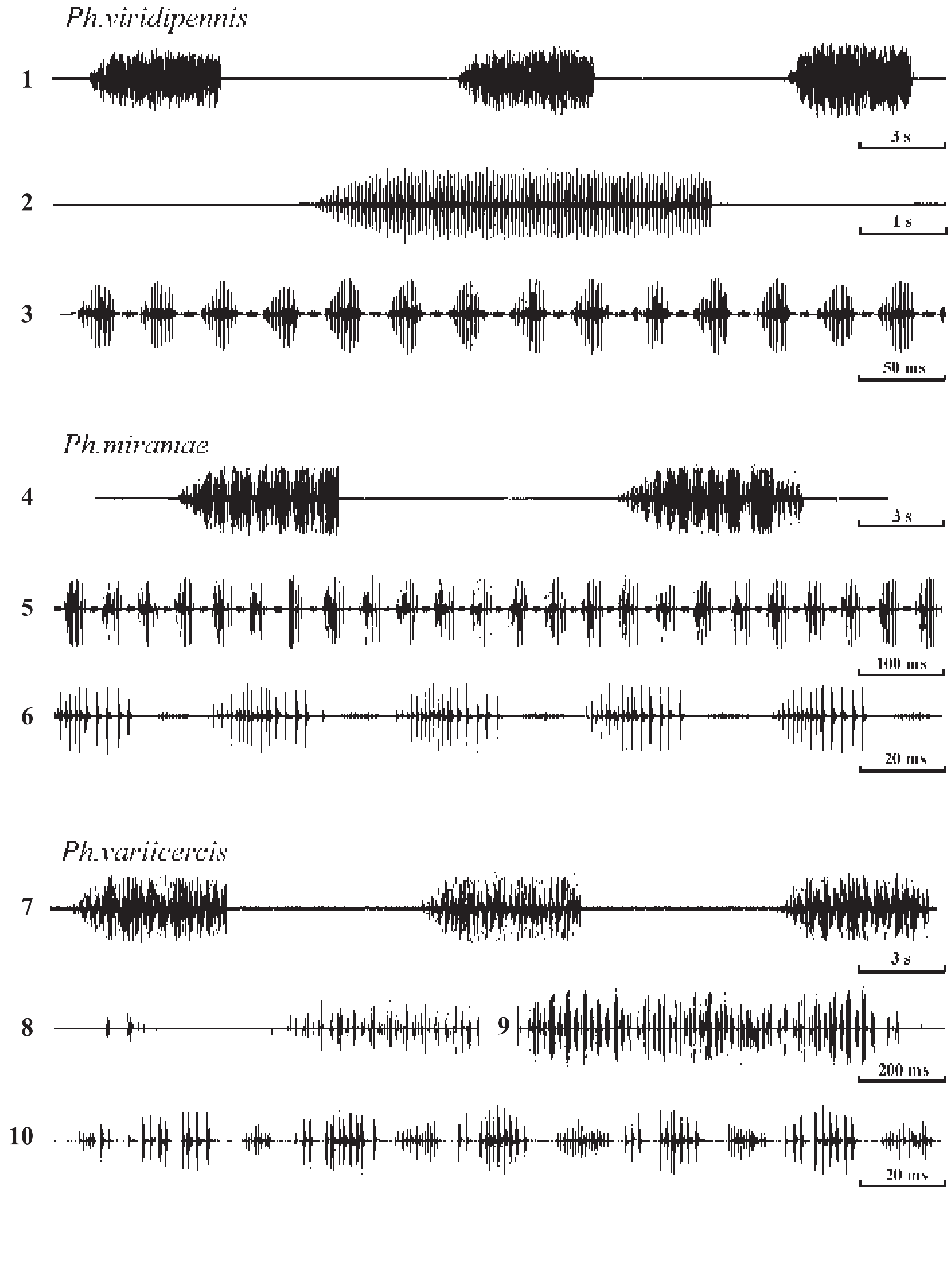
## Results

*Phytodrymadusa viridipennis* (Stshelkanovtsev, 1915)

LOCALITY. Azerbaijan, Talysh, Zuvand, VII.1985.

RECORDING: in laboratory, VIII.1985, recordist O.Korsunovskaya.

SONG. Calling song of single captured male is a very long series lasting 4.5–4.9 s (Figs 1–3, Table 1). They repeat with intervals of 6–8 s. Amplitude of the song increases during the




Figs 1–10. Oscillograms of calling songs of *Phytodrymadusa* spp.: *Ph. viridipennis* (1–3), *Ph. miramae* (4–6), *Ph. variicercis* (7–10) at different velocities. Below time scales.

Рис. 1–10. Осциллограммы призывных сигналов *Phytodrymadusa* spp.: *Ph. viridipennis* (1–3), *Ph. miramae* (4–6), *Ph. variicercis* (7–10) при разных скоростях развертки. Внизу — отметки времени.

Table 1. Temporal characteristics of calling songs of Drymadusini.
Таблица 1. .Временные характеристики призывных сигналов Drymadusini.

| Species | Type of calling song | Phrase | | | Series | | | Closing pulse | | Duration of opening pulse, ms | Temperature, °C |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Duration, ms | Repetition rate, s$^{-1}$ | Number of series | Duration of series or short trills, ms | Repetition rate of series or short trills, s$^{-1}$ | Number of pulses | Duration, ms | Repetition rate, s$^{-1}$ | | |
| *Paradrymadusa galitzini* | periodically repeated series | | | | 247±2 | 1.4–2.6 (mean 1.8) | 11 | 5.1±0.7<br>7.7±0.5<br>10.6±0.4<br>11.7±0.3<br>12.6±0.4<br>13.9±0.3<br>14.3±0.3<br>15.1±0.2<br>15.6±0.3<br>15.9±0.3<br>22.7±0.5 | from 45.7 in the first pulses to 33.6 in the last ones | absent<br>2.1±0.3<br>2.2±0.2<br>2.3±0.1<br>2.5±0.2<br>3.3±0.2<br>3.5±0.1<br>3.7±0.2<br>3.9±0.2<br>4.2±0.1<br>4.7±0.2 | 24 |
| *Anadrymadusa ornatipennis* | periodically repeated series | | | | 97.0±0.6 | 1.8 | 3 | 13.6±0.2<br>14.0±0.2<br>20.2±0.4 | 35.8 | 16.6±0.2<br>10.1±0.2<br>9.6±0.2 | 25 |
| *Anadrymadusa retowskii* | periodically repeated phrases | 398±1 | 1–2.5 | 4–6 | 47.7±0.6 | 14.3 | 2 | 14.7±0.7<br>23.1±0.3 | 40.7 | 7.1±0.4<br>7.7±0.3 | 21 |
| | | | | | 71±1 | 12.8 | | 19.4±0.4<br>28.8±0.4 | 35.8 | 8.3±0.4<br>7.6±0.3 | |
| | | | | | 75.0±0.4 | 12.0 | | 23.6±0.3<br>30.0±0.3 | 31.3 | 10.1±0.5<br>8.5±0.3 | |
| | | | | | 75.9±0.5 | 11.7 | | 24.8±0.3<br>28.2±0.4 | 28.9 | 11.9±0.5<br>8.8±0.3 | |
| | | | | | 74.0±0.6 | | | 24.1±0.4<br>26.1±0.7 | 28.2 | | |
| *A. robusta* | phrases with astable rhythm | 174±4 | 0.5–1.3 | 2 | 73±1 | 12 | 1st series — 1–2,<br>2nd series — 2 | 9.7±0.5<br>28.4±0.7 | 36.2 | 5.7±0.2 | 21 (Ossetia) |
| | | | | | 95±2 | | | 13.2±0.6<br>46.7±0.7 | 27.4 | | |
| | | 258±1 | 1.0 | 2 | 112.0±0.4 | 8 | | 17.8±0.5<br>42.1±0.5 | 23.5 | 13.7±0.6<br>8.2±0.2 | 15 (Daghestan) |
| | | | | | 131.2±0.7 | | | 26.2±0.4<br>63.9±0.9 | 20.7 | 12.4±0.3<br>8.5±0.2 | |

Table 1 (continuing).
Таблица 1 (продолжение).

| Species | Type of calling song | Phrase | | | Series | | | Closing pulse | | Duration of opening pulse, ms | Temperature, °C |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Duration, ms | Repetition rate, $s^{-1}$ | Number of series | Duration of series or short trills, ms | Repetition rate of series or short trills, $s^{-1}$ | Number of pulses | Duration, ms | Repetition rate, $s^{-1}$ | | |
| *A. picta* | phrases with astable rhythm | 131±1 | 1.2–3.3 | 2 | 26.4±0.9<br>83±1 | 14.3 | 1st series —1<br>2nd series — 2 | 13.8±0.7<br>10.7±0.7<br>45.2±0.8 | 36 (in 2nd series) | 6.8±0.5<br>5.4±0.3<br>5.3±0.3 | 21 |
| *A. beckeri* | phrases with astable rhythm | 133±1 | 0.8–1.3 | 2 | 23.8±0.8<br>45.6±0.7 | 11.5 | 1 | 23.8±0.8<br>45.6±0.7 | 11.5 | 2–10**) | 20 |
| *Calopterusa pastuchovi* | trill | | | | | | | 25,9±0,2 | 22.1 | 14,0±0,2 | 26 |
| *Phytodrymadusa viridipennis* | periodically repeated short trills | | | | 4500–4900 | 0.08–0.09 | >150 | 22.7±0.2 | 29 | 7.6±0.1 | 25 |
| *Ph. miramae* | periodically repeated short trills | | | | 4000–6000 | 0.07–0.11 | >100 | 23.9±0.3 | 25 | 10.1±0.4 | 24 |
| *Ph. variicercis* | periodically repeated short trills | | | | 3100–6000 | 0.08 | >100 | 14.8±0.5 | 26–30 | 9.8±0.2 | 24 |
| *Lithodusa daghestanica* | long lasting phrases reminde trills | | | | 111±1 | 7.7 | 3 | 7.9±0.3<br>6.8±0.2<br>9.2±0.3 | 27.5;<br>21.2 | 9.3±0.2<br>10.7±0.3<br>23.4±0.4 | 20 |
| *Atlanticus brunneri* | periodically repeated series | | | | 69.8±0.8 | 10 | 3 | 13.2±0.2<br>15.5±0.2<br>16.9±0.2 | 45.5 | 5.7±0.3<br>3.3±0.2<br>3.9±0.1 | 21 |
| *Eulithoxenus mongolicus* | periodically repeated series | | | | 65.4±0.8 | 1.5–2 | 2 | 18.1±0.5<br>29.4±0.6 | 30 | absent | 24 |

*) The mean and mean error are given; number of measurements is 15-20. In the case, when the variability of a signal is significant, the limits of measurements are given. Mean without a error are given when the specified data were observed more, than in 80 % of cases.
**) There is given duration of micropulses in pauses between two macropulses of series.

first second. Sound is produced by both opening and closing movements of the tegmina. The closing pulse is louder and slower than the opening one. Each closing pulse consists of 15–18 separate tooth-impacts. Their amplitude increases gradually the first 2/3 of the pulse and decrease more rapidly in final 1/3 of the pulse. Duration of closing pulse is 22.7±0.2 ms, opening pulse — 7.6±0.1 ms, interpulse interval — 11.5±0.2 ms. Pulse rate at 25 °C is about 29 $s^{-1}$.

The most frequency components lay in the range of 10–50 kHz (Fig. 23). The frequency spectrum contains two main peaks: the first one is near 16–18 kHz, and the second one — near 22–24 kHz. The spectrum of opening pulses differs from the closing pulses spectrum by absence of the first frequency maximum.

### *Phytodrymadusa miramae* (Uvarov, 1929)

LOCALITY. Armenia, near Wedy, E of Gorovan Village, stony desert, 13.VII.2000.

RECORDING in the laboratory (one male), recordist O. Korsunovskaya; in the field (one male), recordist V. Savitsky.

SONG of this species is pulse sequencies repeating rather regularly during continuous calling. It is possible to consider them as very long series or short trills (Figs 4–6, Table 1). Their duration is 4–6 s, intervals between them are 3–10 s. Each series contains more than 100 pairs of low amplitude opening and loud closing pulses. The amplitude of pulse sequency achieves maximum in 1.5–2 s. In beginning part of the song when amplitude of tegmina motion is very low, the wing opening is soundless. In the middle part of trill opening pulses last about 10 ms. Each closing pulse lasts approximately 24 ms and contains ca 20 separate tooth-impacts. Frequency of last 5–6 of them is significantly less than of previous ones. Pulse rate is about 25 $s^{-1}$ at 24°C.

Frequency spectrum lays between 0.1 and 50 kHz (Fig. 24). Dominant frequencies are 18–21 kHz. There are some additional peaks at 25 and significant more low near 31, 36 and 43 kHz. In low frequency part of spectrum there is a small maximum near 0.6–0.9 kHz apparently reflecting frequency of tooth-impacts inside pulses. It is observed weak frequency modulation in the song. During opening pulse dominant frequency is near 18 kHz and there is low peak at 25–26 kHz, the first fast part of closing pulse has the same spectrum, but in second part with less frequency of clicks dominant frequency is displaced to the left part of spectrum and becomes about 19–22 kHz (in different pulses).

### *Phytodrymadusa variicercis* (Veltistshev, 1937)

LOCALITY. Eastern Armenia, S of Goris Town, gorge of river Worotan, 1000 m, 11.VII.2000.

RECORDING in the laboratory (one male), recordist O. Korsunovskaya.

One male was captured during last larval instar and imaginal moult occured in laboratory. HisCALLING SONG one can listen in the night only. These sounds as in other studied species of the genus were pulse trains with increased in half or one s amplitude (Fig. 7). These sequencies repeat rather regularly during continuous calling. Their duration varied between 3.1 and 6 s and interval between trains was 5.9–7.5 s (Table 1). Most of pulse trains consists of more than 100 (usually about 150–200) pairs of opening and closing pulses. There are several clicks or fast pulses before each train (Fig. 8). Interval between these initial units and pulse sequency usually is no more than 300 ms. The pulse train ends by opening pulse and after pause of ca 25 ms by one or two pulses with lower amplitude (Fig. 9). Mean duration of opening and closing pulses in the middle part of pulse train are 9.8 and 14.8 ms respectively. The closing pulses as a rule consist of two parts, the first of them contains 2–4 tooth-impacts and lasts about 2–8 ms. Sometimes this part may be absent, the second part is more longer and consists of up to 8 tooth-impacts. Its duration is about 5–10 ms (Fig. 10). High level of variability is peculiar to closing pulse duration in the song of investigated male. Very often tooth-impact number in this unit is reduced, and two parts of pulse become almost indistinguished. The rhythm and duration of opening pulses are more stable.

Frequency spectrum occupies range between 10–13 and 70 kHz (Fig. 25). The spectrum of the closing pulse contains several peaks. The main is at 17–20 kHz (the first part of pulse) or 28–32 kHz (the second part), the others there are at 24–25 and 27–28 kHz. Frequency content of opening pulse differs from the closing one. The first peak (at 17–20 kHz) absents and the maximal amplitudes of frequency components are observed at 27 kHz. The spectrum of first loud pulse before series coincides or very similar to spectrum of opening pulse. It occupies frequency band between 10 and 45 kHz and contains only one maximum at 25 kHz.

### *Calopterusa pastuchovi* (Uvarov, 1917)

LOCALITY. Aserbaijan, Lerik, VI.1987.

RECORDING: in laboratory, one male, recordist O. Korsunovskaya

SONG. Calling song of this species is long lasting trill which consists of both opening and closing pulses (Figs 11, 13). Duration of closing pulses is 25.9±0.2 ms, opening ones — 14.0±0.2 ms, interpulse interval — 19.4±0.2 ms. The pulse rate is about 22 $s^{-1}$ at 26°C (Table 1).

Besides trills the male produced short series composed of two opening and closing pulses (Figs 12, 14). The pulse repetition rate in these series is very close to the one in calling trill, but series repeat with different interval duration, often more than several minutes, usually they are produced in reply to another acoustic stimuli (e.g sounds of other bush crickets). We consider that these sounds may have function of territorial signals. Similar type of sounds is known in *Gampsocleis* spp.

The noisy spectra of calling and territorial signals contain several maxima: main peak is near 12 kHz, the next ones are at 15–19 and 27 kHz (Figs 26, 27). Dominant frequency in the opening pulse spectrum is 27 kHz.

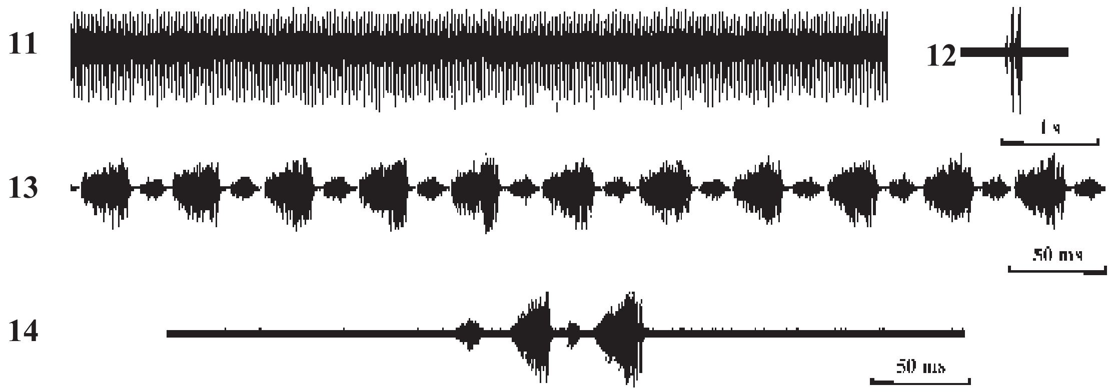
### *Lithodusa daghestanica* Bey-Bienko, 1951

LOCALITY. Daghestan, near Gunib Village, 1000 m, 9.VIII.1997.

TAPE RECORDS: in laboratory (two males, recordist O. Korsunovskaya) and in the field (one male, recordist V. Savitsky).

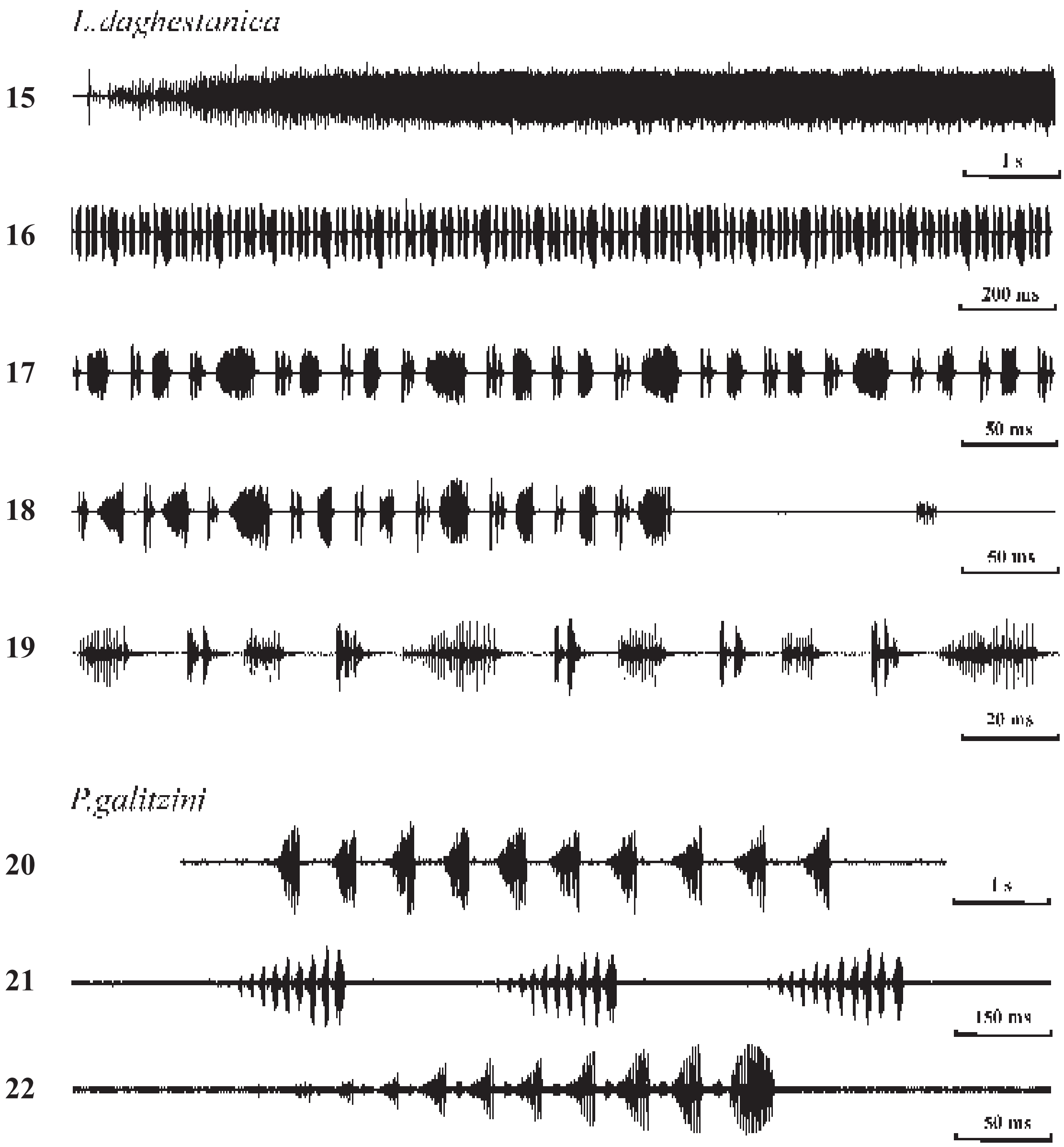
These bush crickets were captured at bottom of a rock on small area of rugged stones arisen as a result of erosion. Insects, both males and females, were hidden in stones. Neighboures of *Lithodusa* in their habitats were *Platycleis daghestanica*, males of this species produce trills as calling signal.

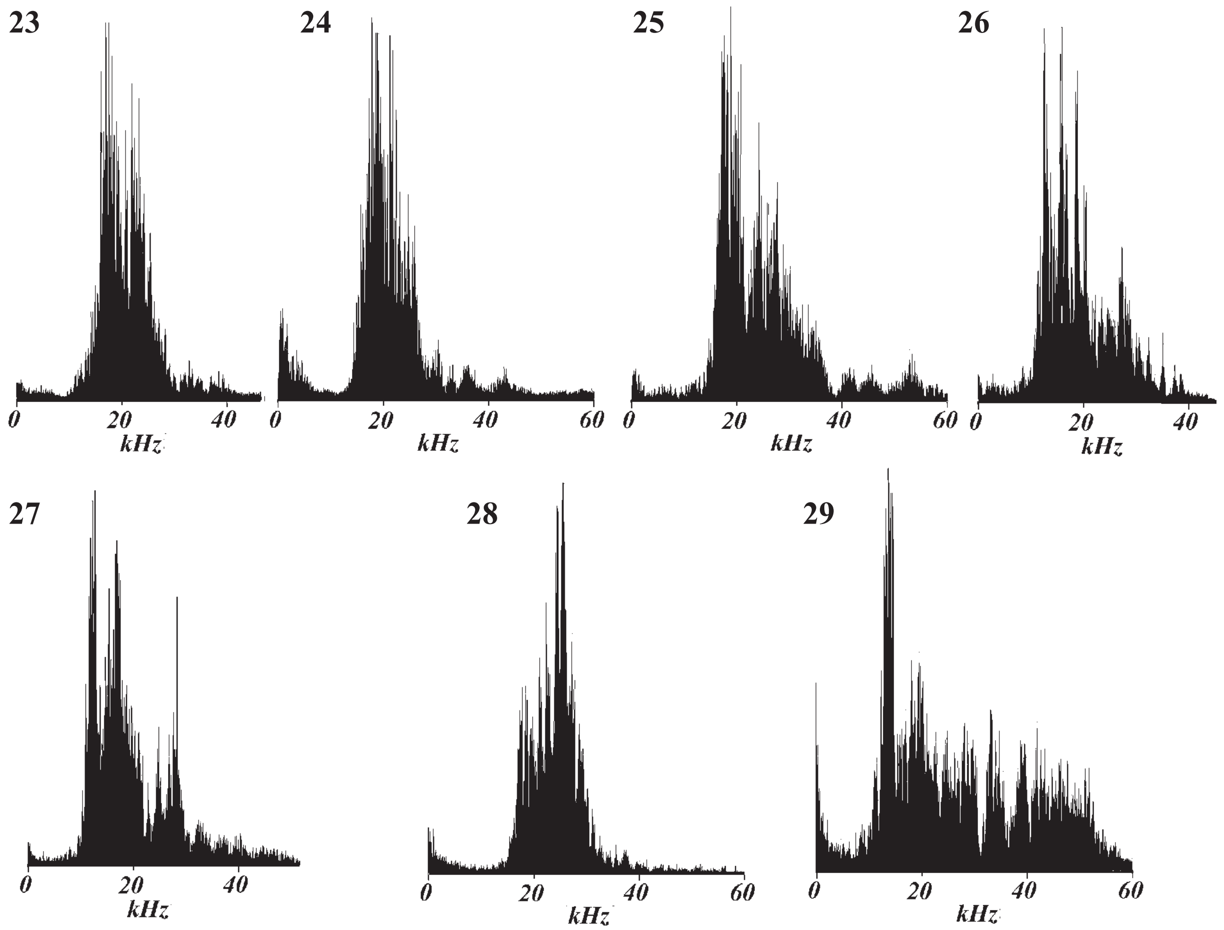
SONG. Males of *Lithodusa daghestanica* produce long trains of sound pulses (after our observations up to 1 min). Their temporal pattern is complex and can be considered as a sequence of series consisting of three pairs pulses (opening




Figs 11–14. Oscillograms of calling (11, 13) and territorial (12, 14) signals of *Calopterusa pastuchovi* at different velocities. Below time scales.

Рис. 11–14. Осциллограммы призывных (11, 13) и территориальных (12, 14) сигналов *Calopterusa pastuchovi* при разных скоростях развертки. Внизу — отметки времени.






Figs 23–29. Power spectra of sound signals at complete cycle of tegmina movements during stridulation of *Phytodrymadusa*, *Calopterusa* and *Lithodusa* spp.: 23 — calling song of *Ph. viridipennis*, 24 — ditto, *Ph. miramae*, 25 — ditto, *Ph. variicercis*, 26 — ditto, *C. pastuchovi*, 27 — territorial signal of *C. pastuchovi*, 28 — calling song of *Lithodusa daghestanica*, 29 — ditto, *Paradrymadusa galitzini*. Vertical scales are linear.

Рис. 23–29. Амплитудно-частотные спектры звуковых сигналов при полном цикле движений надкрылий при стридуляции *Phytodrymadusa*, *Calopterusa, Lithodusa* и *Paradrymadusa* spp.: 23 — призывный сигнал *Ph. viridipennis*, 24 — то же *Ph. miramae*, 25 — то же *Ph. variicercis*, 26 — то же *C. pastuchovi*, 27 — территориальный сигнал *C. pastuchovi*, 28 — призывный сигнал *Lithodusa daghestanica*, 29 — то же *Paradrymadusa galitzini*. Вертикальная шкала в линейном масштабе.

and closing) (Figs 15–19, Table 1). The train begins with a fast loud single pulse, then weak clicks follow. Their amplitude and duration gradually increase and achieves a maximum in 2 s. Each series includes opening pulses of different duration. The first and the second ones last at 20°C about 10 ms (mean 9.3±0.3 and 10.7±0.3 ms respectively), duration of the third pulse is maximal in the chirp (23.4±0.4 ms). Mean intervals between $1^{st}$ , $2^{nd}$ and $3^{rd}$ closing pulses are 26.3 and 40.6 ms respectively, but interval between 3rd and next pulse is about 27 ms. Each opening pulse followed by fast loud closing pulse (mean duration is 7.9, 6.8 and 9.2 ms respectively) consisting of two-four well distinguished separated clicks. So pulse repetition rate is 21.2 in the beginning of series and 27.5 $s^{-1}$ in the end of it. Series repetition rate is 7.7 $s^{-1}$. Calling song finish by loud opening pulse and with pause of about 130–150 ms more silent closing one (Fig. 18). Similar end of singing everyone can observe in *Tettigonia* and many other species when insect suddenly disturbed during stridulation. Closing of tegmina can be heard as a single click even in minutes after end of singing.

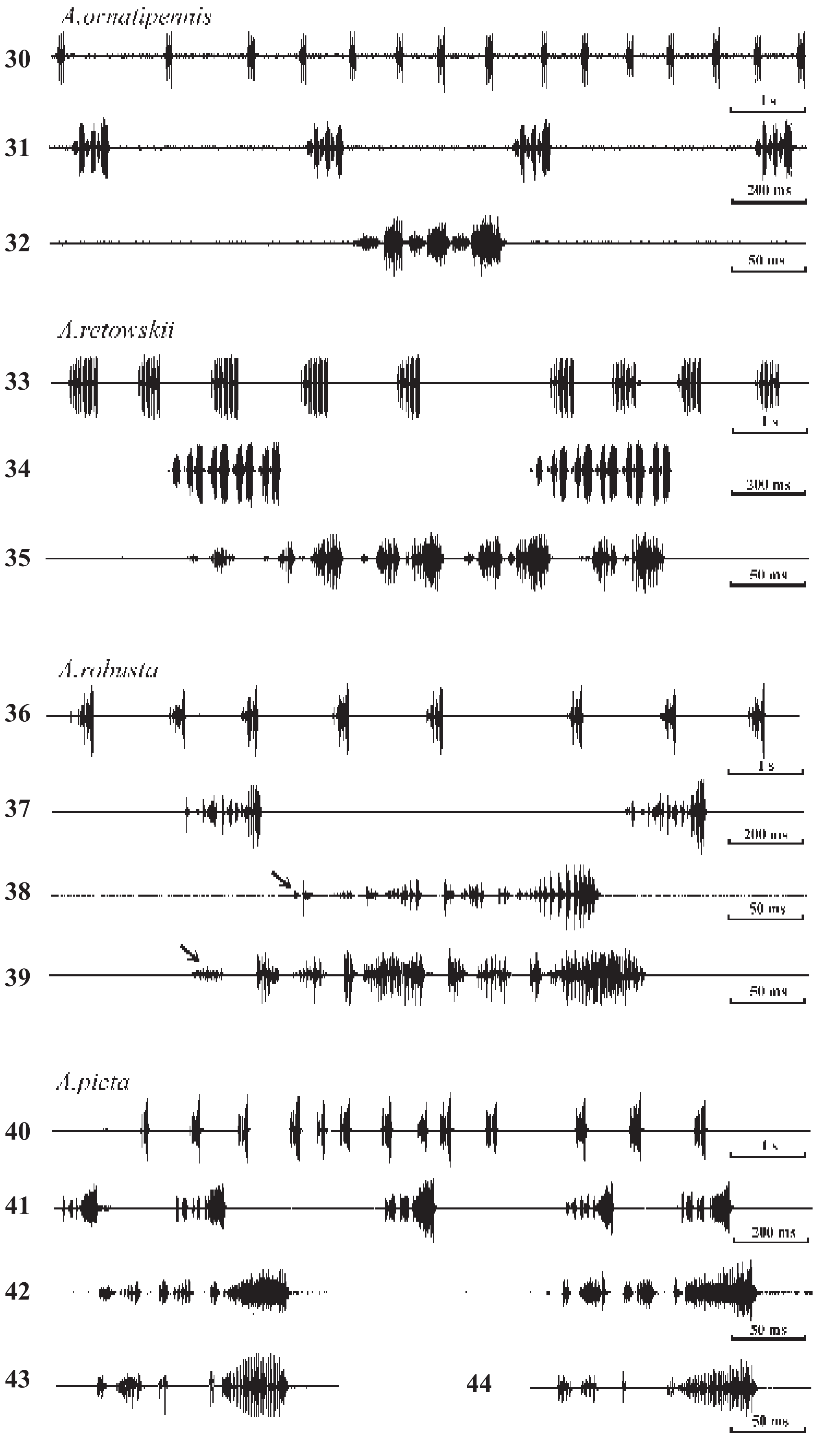
Frequency spectrum of calling song (Fig. 28) occupies a range between 13 and 40 kHz and coincides with the spectrum of the opening pulses. Main peak is near 26 kHz, the minor maximum is at 16–20 kHz. Spectrà of closing pulses differ from the spectra of closing pulses by absence of low frequency peak.

### *Paradrymadusa galitzini* Retowski, 1888

LOCALITIES. Eastern Crimea, near Sudak, one male, VIII. 1969, two males, 25.VIII.1985; Krasnodar Territory, W coast of Black Sea, Arkhipo-Osipovka Village, VIII.1986, one male.

Figs 15–22. Oscillograms of calling songs of *Lithodusa daghestanica* (15–19: 15 — the first 10 s of song; 16, 17, 19 — the middle part of the song, 18 — the end of the signal) and *Paradrymadusa galitzini* (20–22) at different velocities. Below time scales.

Рис. 15–22. Осциллограммы призывных сигналов *Lithodusa daghestanica* (15–19: 15 — первые 10 с сигнала; 16, 17, 19 — середина, 18 — конец сигнала) и *Paradrymadusa galitzini* (20–22) при разных скоростях развертки. Внизу — отметки времени.


A.ornatipennis
30
1 s
31
200 ms
32
50 ms
A.retowskii
33
1 s
34
200 ms
35
50 ms
A.robusta
36
1 s
37
200 ms
38
50 ms
39
50 ms
A.picta
40
1 s
41
200 ms
42
50 ms
43
44
50 ms

RECORDING: in laboratory, three males, recordists: R. Zhantiev, N. Dubrovin, O. Korsunovskaya.

SONG. Bush-crickets produce their calling signal at night only. The song consists of long lasting sequences of series, each of them is formed by 11–12 closing pulses and lasts about 250 ms (Figs 20–22). Repetition rate of series is 1.4–2.6 $s^{-1}$, pulse repetition rate decreases from 45.7 $s^{-1}$ in the beginning of series to 33.6 $s^{-1}$ in the end of it (24°C) (Table 1). Amplitude of pulses gradually rises to the end of the chirp. Each closing pulse consists of separate tooth-impacts and is preceded by low amplitude opening pulse. The main peak in spectrum of complete cycle of tegmina movements during stridulation (Fig. 29) lying in the range 8–55 kHz coincides with dominant frequency of closing pulses spectrum (14 kHz). Main peak in opening pulses spectrum is at 46 kHz.

The calling song of this species is very similar to the sound signal of mediterranean species *Paradrymadusa aksirayi* [Heller, 1988].

### *Anadrymadusa ornatipennis* (Ramme, 1926)

LOCALITY. Turkey, near Marmaris, 21.VI.2001, one male.

RECORDING were made in laboratory at 25°C; recordist O. Korsunovskaya.

For the first time calling song and movements of tegmina of this species was recorded by K.-G. Heller [1988] but the bushcricket was captured in Greece (isl. Rhodos). Our specimen was captured during last larval instar and imaginal moult occured in laboratory. His CALLING SONG as well as at specimen from Greece consist of repeating three-pulsed series (Figs. 30–32). Each loud closing pulse is preceeded by low amplitude opening pulse. Duration of opening pulses decreased from 16.6 (1st pulse) to 9.6 (3rd pulse), but duration of closing pulses increases to the end of series from 13.6 to 20.2 ms. Intervals between closing pulses are about 14 ms. Pulse repetition rate is ca 36 $s^{-1}$ (Table 1). Series duration is stable (from 94 to 103 ms). Interval between series can vary over a wide range, but during continuos stable night calling series repetition rate is ca 1.8 $s^{-1}$ (at 25°C) (Fig. 30).

Spectrum of the song occupies the range between 0.5 and 55 kHz (Fig. 59). Dominant frequency of opening pulse is near 20 kHz, there are two additional lower peaks at 17 and 35 kHz, the closing pulse gives spectrum with two maxima only: the main one is at 16 kHz and the second one at 33 kHz.

### *Anadrymadusa retowskii* (Adelung, 1907)

LOCALITY. Eastern Crimea, near Sudak, VIII.1968, 25.VIII.1985, three males; Eastern Crimea, Karadagh, Echkidagh, 30.VIII.1997, four males.

*Anadrymadusa retowskii* is endemic species, known from Eastern Crimea only. All bush crickets were captured in dry habitats of Karadag and near vicinities. Usually their loud songs can be heard at night. Males sing in low bushes, separated one by another in several tens meters. But in summer 1997 one of us observed unusual great density of these bush crickets. They were acoustically active in day light too. The singing males were sitting on or near the ground in low bushes. Distance between insects was no more than 10–15 m. Females were active too and went to calling males.

RECORDINGS were made in laboratory and in the field. Recordists: R. Zhantiev, N. Dubrovin, O. Korsunovskaya.

THE SONG has a complex rhythmic pattern (Figs 33–35, Table 1). 5 or 6 two-pulsed series join in groups, they in turn form sequences lasting indefinitely (as a rule more than a minute). The first series in group lasting about 50 ms consists of two pulses only (opening and closing) and its amplitude is lower than in following series. Each closing pulse is preceded by fast low-amplitude opening pulse. The pulse repetition rate decreases from 40.7 (1st series) to 28. 2 $s^{-1}$, series repetition rate is 13.5 (1st series) and 11.7 (last series) $s^{-1}$. Series sequences are produced with frequency of about 1 $s^{-1}$ (at 21 °C). The mean pulse duration rises during each series sequence from 14.7 to 24.8 and from 23.1 to 30 ms of the first and the second pulses respectively. Series duration in the phrases are different too. It is minimal in the first series (47.7±0.6 ms) and reaches maximum to the fourth series (75.9±0.5 ms) (Table 1).

In the frequency spectrum (Fig. 60) there are main peak at 15–16 kHz and the several additional maxima at 12, 17 and 20–22 kHz. Spectra of opening and closing pulses are different: dominant components during opening of tegmina are near 20–21 kHz and during closing of them the more low frequencies (12–13 kHz) add. The dominant frequencies appear at 15–18 kHz.

### *Anadrymadusa robusta* (Miram, 1926)

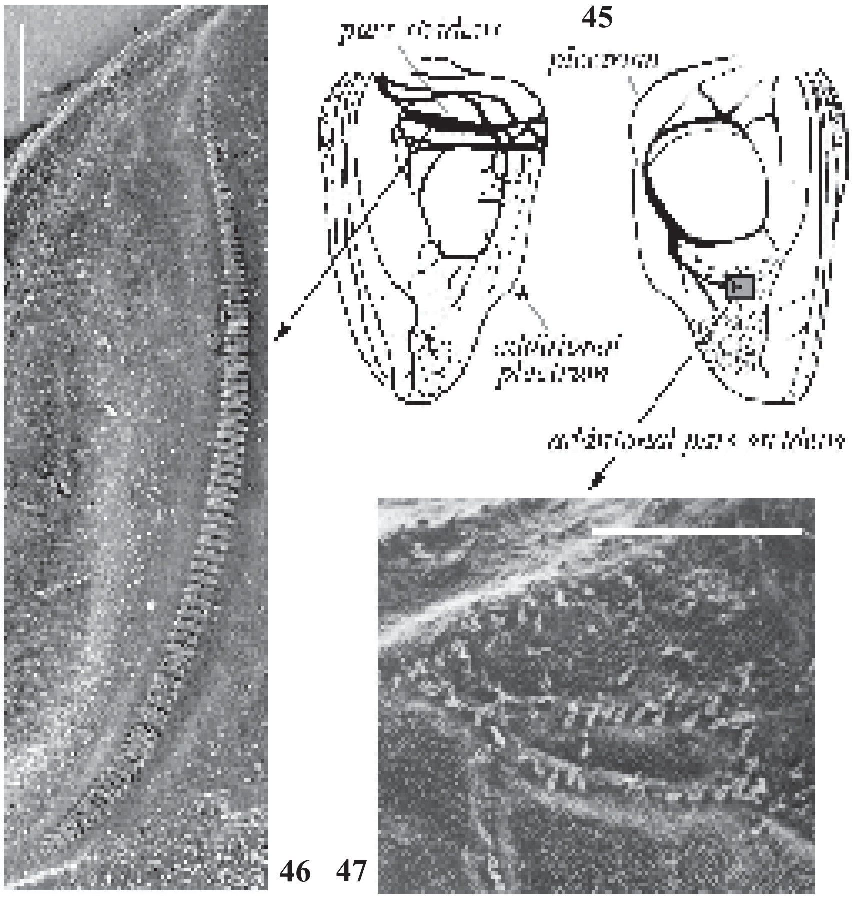
LOCALITIES. Northern Caucasus: North Ossetia, Alagir Distr., near Zintsar Village, 24.IX.1985; Daghestan: Bogossky Range, 1200 m, 31.VII.1997.

RECORDINGS were made in the laboratory (two males from Ossetia, recordist O. Korsunovskaya) and in the field (Daghestan, one male), recordist V. Savitsky.

Males of *A. robusta* produce CALLING SIGNALS with complex temporal pattern (Figs 36–39). There are rather regularly repeated phrases separated one of another with pauses of 560 ms (21°C). Duration of intervals between these phrases depends on temperature and motivation of the male. Each phrase has a complicated pattern of sound pulses of different duration and amplitude. Careful analysis of oscillograms and spectra of different parts of the song shows that the phrase can be divided into two series consisting of two opening and two closing pulses (Figs 38–39). The first closing pulse in each series is faster than the subsequent one. Their mean duration at 21°C is in the first series 9.7 and 28.4 ms, in the second — 13.2 and 46.7 ms respectively. The amplitude

Figs 30–44. Oscillograms of calling signals of *Anadrymadusa* spp. at different velocities: 30–32 — *A. ornatipennis,* 33–35 — ditto, *A. retowskii*, 36–39 — ditto, *A. robusta* (36–38 — male from North Ossetia at 21°C; 39 — phrase of the male from Daghestan at 15°C, record was made with AVLS to reveal of low amplitude elements of signal pattern, arrows show the initial sound pulse probably produced by the the tegminal closing apparatus; 40–44 — calling signal of *A. picta* (43, 44 — two phrases of the same male and the same velocity as in Fig. 42 with incomplete pattern); below time scales.

Рис. 30–44. Осциллограммы призывных сигналов *Anadrymadusa* spp. при разных скоростях развертки: 30–32 — *A. ornatipennis,* 33–35 — то же *A. retowskii*, 36–39 — то же *A. robusta* (36–38 — самец из Северной Осетии при 21°C; 39 — фраза самца из Дагестана при 15°C, запись сделана с автоматической регулировкой уровня звука для выявления низкоамплитудных элементов паттерна сигнала, стрелками показан начальный звуковой пульс, возможно, продуцируемый замыкательным аппаратом надкрылий; 40–44 — призывный сигнал *A. picta* (43, 44 — две фразы с неполным паттерном того же самца при той же скорости развертки, что и на рис. 42); внизу — отметки времени.



Figs 45–47. Elytra and different parts of stridulatory and closing apparata of *A. robusta* (North Ossetia): 45 — left and right elytra of the male from above. Asterisk shows in the left elytron the sclerotized edge which most likely is used at sound production when elytra open. Darkened square in the right wing represents the part of closing apparatus with veins bearing small spines on their upper surface and corresponds to Fig. 47; 46 — stridulatory file (*pars stridens* in Fig. 45) of the left elytron, 47 — fragment of closing apparatus of the right elytron. Scales 500 mkm (46, 47).

Рис. 45–47. Надкрылья и различные части стридуляционного и замыкательного аппаратов *A. robusta* (Северная Осетия): 45 — левое и правой надкрылья самца сверху. Звездочкой на левом надкрылье показан склеротизованный край, который, вероятно, используется при издавании звука во время открывания надкрылий. Затемненный квадрат на правом надкрылье обозначает часть замыкательного аппарата с жилками, несущими на дорсальной поверхности мелкие шипики, и соответствует рис. 47; 46 — стридуляционная жилка (*pars stridens* на рис. 45) левого надкрылья, 47 — фрагмент замыкательного аппарата правого надкрылья. Масштаб 500 мкм (46, 47).

of pulses rises to the end of phrase. Intervals between closing pulses are about 18 and 23 ms. Opening pulses is of the higher amplitude than in most of other Tettigoniids. As a rule fast low amplitude micropulse is well distinguished before phrase (Figs 38, 39). We believed that this sound is produced by means of any of other stridulatory structure. The possible candidate was closing apparatus of tegmina: small pegs on dorsal surface of veins in distal part of downer tegmen (Figs 45, 47). To examine this idea we extirpated *plectrum* and thus have excluded an opportunity to use in stridulation the greatest part of *pars stridens*. After this operation male could produce some sounds without usage stridulatory file. The closing apparatus of tegmina apparently is very important in sound production because extirpation of this structure destroys the temporal pattern of calling song and changes resonant properties of downer tegmen.

The spectra of closing pulses in two chirps are similar (Fig. 48). The dominant frequency is about 12–14 kHz in the first series and 9–14 kHz in the second one. There is significant peak at 6–7 or 9 kHz. Besides these maxima there is additional peak at 25–26 kHz in the spectra of the second closing pulses of both series. This peak in last closing pulse of the phrase of the same amplitude, as first at 12–14 kHz. The frequency contents of the 2nd, 3rd and 4th opening pulses are very similar too. Their spectra contain components of high amplitude in more high frequency range than in closing pulse ones. Significant maxima appear at 11–13, 18, 21–22 and 26 kHz. As a rule in the beginning of the phrase pulse amplitude is low and in this case spectra of opening and closing pulses are identical or close to the frequency spectrum of a small pulse before them. The spectrum of sound produced by complete cycle of tegmina movements during stridulation is given in Fig. 61.

Some males move their tegmina with lower amplitude and the first closing pulse in phrase may absent. In this case phrase consists of three closing pulses, the middle of them is faster and more silent.

### *Anadrymadusa picta* Uvarov, 1927

LOCALITY. Daghestan, W of Makhachkala Town, Karatoebe Range, near Barkhan Sarykum, 150 m, 11–16.VII.1997.

TAPE RECORDS were made in the field by V. Savitsky.

SONG. The males produced calling signal during several seconds with intervals sometimes achieving several minutes. There are three-pulsed series with repetition rate of one per *s* (at 20–21°C) (Figs 40–42, Table 1). The temporal pattern is very close to the one of *A. robusta*, if this species produce incomplete phrases without the first pair of opening and closing pulses. There are high amplitude opening pulses, duration of closing pulses increases to the end of each chirp. But amplitude of second pulse is the same as well as the first one and if a chirp is incomplete, the second pulse is absent (Figs 43, 44). Each series lasts 120–130 ms and closing pulses 13.8, 10.7, 45.2 ms respectively. Opening pulse duration is between 3 and 10 ms (mean 6.8, 5.4 and 5.3 ms respectively). Pulse repetition rate is 26–28 $s^{-1}$. Interval between 1st and 2nd closing pulses is longer than between 2nd and 3rd ones (20.5±0.8 and 16.8±0.6 ms respectively). This apparently means that

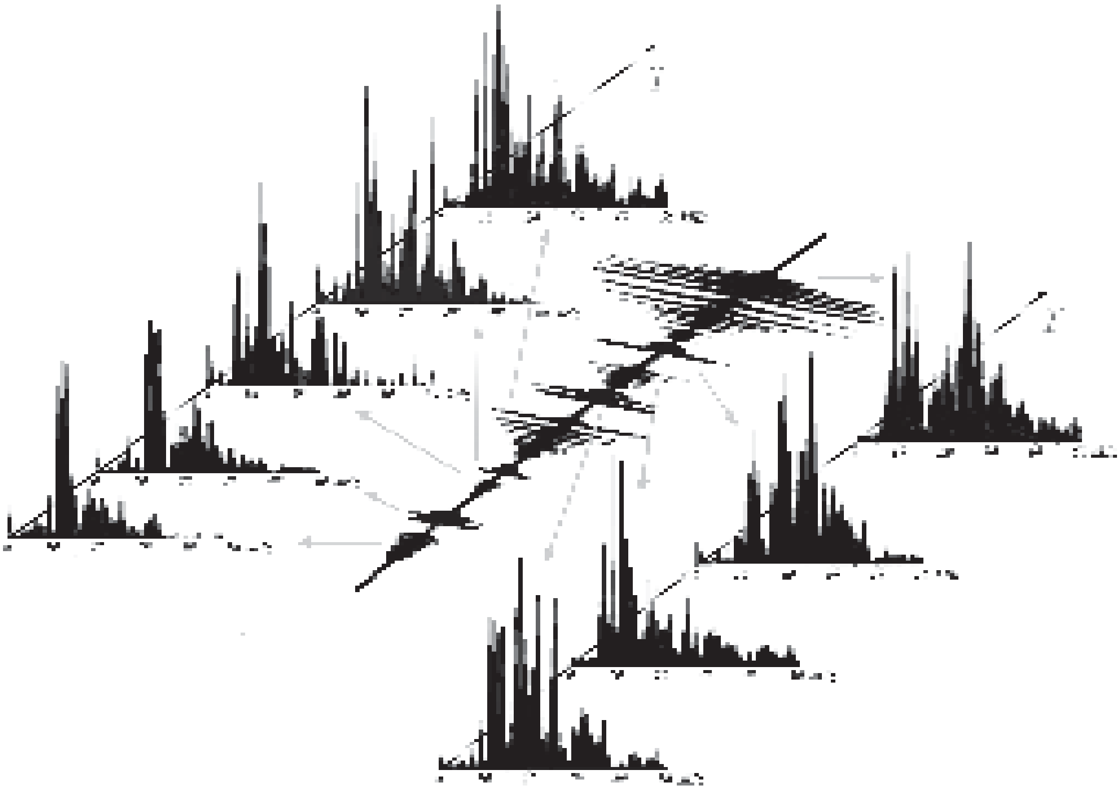


Fig. 48. Power spectra in linear scale of different parts of calling song of *A. robusta* (North Ossetia). T — time.

Рис. 48. Амплитудно-частотные спектры в линейном масштабе различных частей призывного сигнала *A. robusta* (Северная Осетия). T — время.

males of *A. picta* produce not three-pulse series but a phrases consisting of two series — the first of them contains one pair of opening and closing pulses only and the second one consists of two pairs of pulses of rising amplitude. The low amplitude sound unit before each phrase if exists is faster than in *A. robusta* (area with pegs on tegmen in *A. picta* is smaller than in *A. robusta*).

### *Anadrymadusa beckeri* (Adelung, 1907)

LOCALITY. SE Daghestan, S of Akhty Village, 1200–2000 m, 14.VIII.1997.

TAPE RECORDS were made in laboratory (one male, recordist O.Korsunovskaya) and in the field (two males, recordist V.Savitsky).

SONG of these insects (Figs 49–51) is sequence of two-pulsed chirps lasting several seconds. Series last about 130–140 ms and were produced with different periods. Minimal was 708 ms and maximal one (in sequence of series) 1.2 s. The first pulse of the chirp is faster than the second one (23.8±0.8 ms vs 45.6±0.7 ms) (Table 1), interval between pulses lasts 50–60 ms. Several low amplitude short clicks were distinguished in pause after first pulse. They last from two to 10 ms. The frequency analysis shows that spectra of the loud pulses are very similar. They contain three maxima at 11, 17–19 and 26–30 kHz. Spectrum of minor pulses does not contain high peak at 10–11 kHz (Fig. 58). The spectrum of sound produced by complete cycle of tegmina movements during stridulation is given in Fig. 62.

### *Eulithoxenus mongolicus* (Uvarov, 1928)

LOCALITY. S Siberia, S Tuva, near Erzin, 13.IX.1986. One male was captured on a stony slope of a hill with low and rarefied vegetation.

RECORDING was made in laboratory (recordist O. Korsunovskaya).

Type of CALLING SONG of this species is very similar to the same signal of *Anadrymadusa beckeri. E. mongolicus* produces two-pulsed series (Figs 52–54). The first pulse is shorter (ca 20 vs 30 ms) and more silent than the second one. However in *E. mongolicus* interval between pulses does not contain micropulses as it is observed in *A. beckeri*. Pulse repetition rate is about 30 $s^{-1}$, series repetition rate about 2 $s^{-1}$ (Table 1).

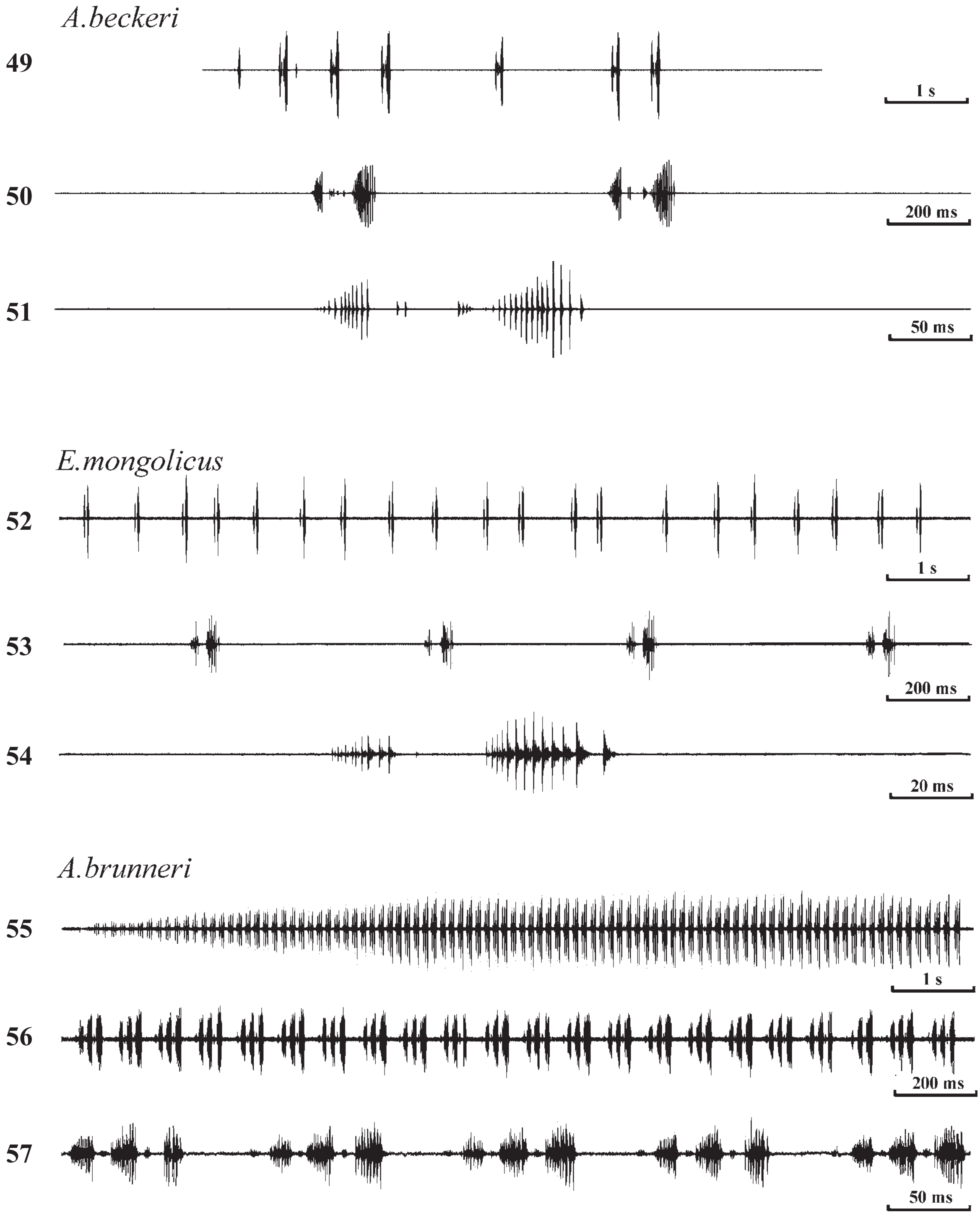
As in *A. beckeri* two pulses in series of *E. mongolicus* have the same spectra. The main frequency peak occupied the band between 20 and 27 kHz with maximum at 22 kHz; additional peak is near 30 kHz (Fig. 63).

### *Atlanticus brunneri* (Pylnov, 1914)

LOCALITY. S Maritime Territory, Khasan Distr., near Ryazanovka Station, 3–10.IX.2000.

RECORDING of the song (one male) was made in laboratory (recordist O. Korsunovskaya).

Male produced CALLING SONG in darkness only and sang through all night. This signal is a sequence of three pulsed series lasting from several seconds up to several minutes (Figs 55–57, Table 1). Mean duration of series is 70




Figs 49–57. Oscillograms of calling songs of *Anadrymadusa beckeri* (49–51), *Eulithoxenus mongolicus* (52–54) and *Atlanticus brunneri* (55–57) at different velocities. Below time scales.

Рис. 49–57. Осциллограммы призывных сигналов *Anadrymadusa beckeri* (49–51), *Eulithoxenus mongolicus* (52–54) и *Atlanticus brunneri* (55–57) при разных скоростях развертки. Внизу — отметки времени.

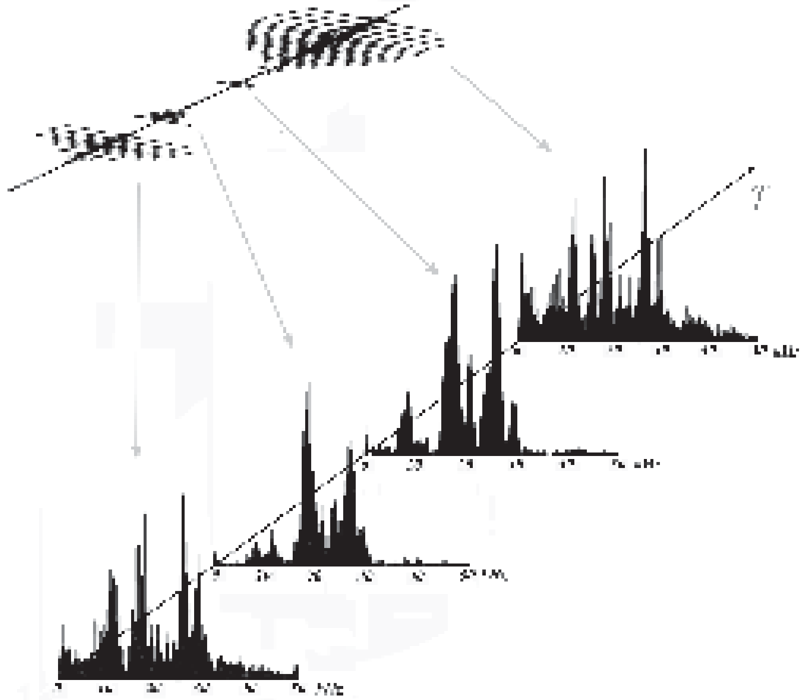


Fig. 58. Power spectra in linear scale of different parts of calling song of *A. beckeri*. T — time.

Рис. 58. Амплитудно-частотные спектры различных частей призывного сигнала в линейном масштабе *A. beckeri*. T — время.

ms, intervals between them 32 ms, the first closing pulse in the series is slightly faster than two subsequent ones but the first opening pulse has maximal duration (5.7 ms). Short intervals between pulses last ca 7 ms. Pulse repetition rate in series is 45–50 $s^{-1}$, series repeat with frequency about 10 $s^{-1}$.

The frequency spectrum occupies range between 10 and 50 kHz. There are main peak at 16 kHz and the additional ones at 12–13, near 29 and 35 kHz (Fig. 64).

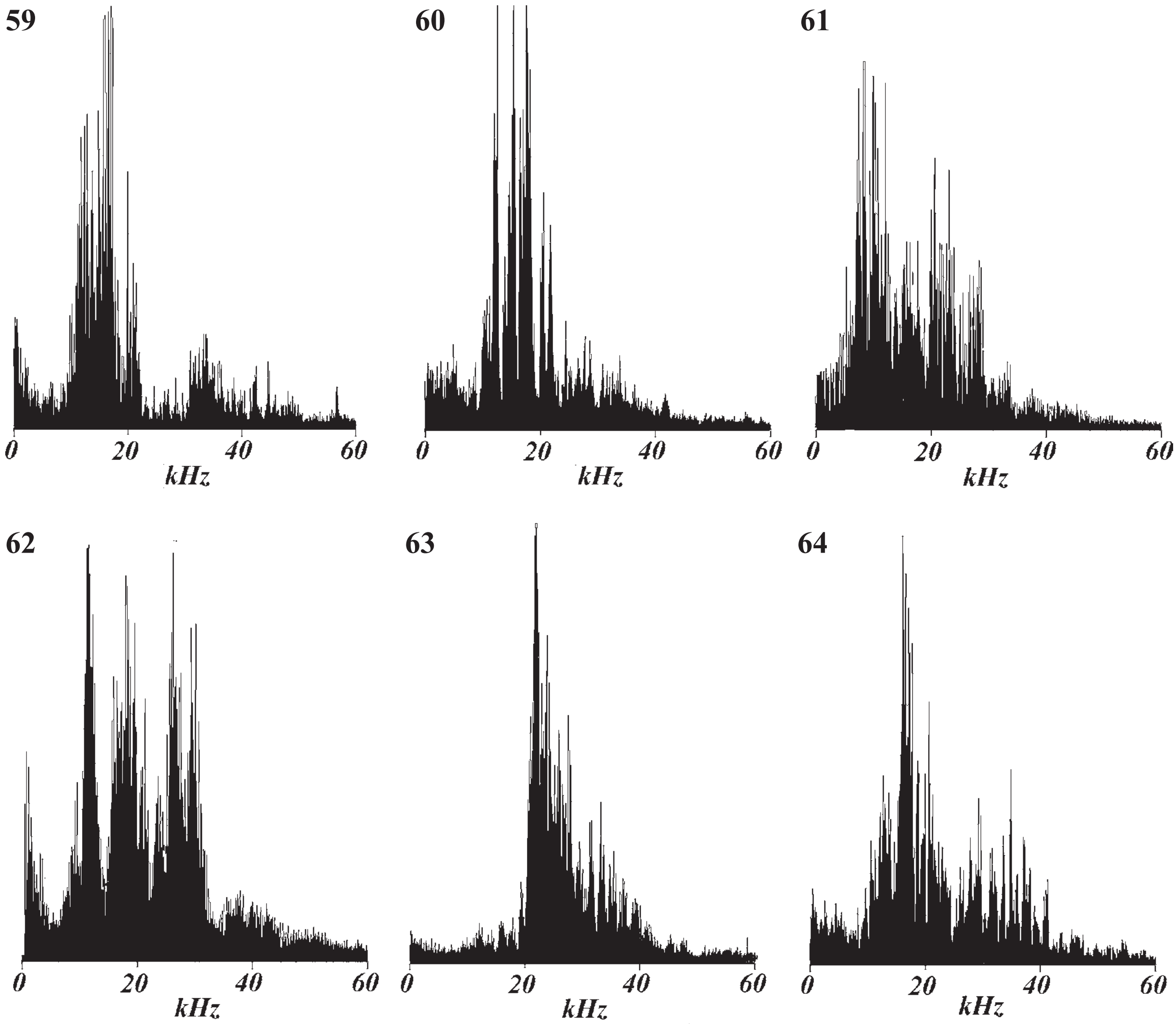
## Discussion

The comparative analysis of calling signals investigated Drymadusini bush crickets has shown, that they can produce sounds with very complex temporal structure. So, alongside *Calopterusa* and one of nearctic *Atlanticus* species [Walker, Moore, 2001] producing trills — the signals with one rhythmic level — exist species with calling signals with up to three rhythmic levels. They are *Anadrymadusa retowskii, A. robusta*, *A. picta* and *Atlanticus gibbosus*. Rhythm of the first order is represented by pulse repetition rate, rhythm of the second order — repetition rate of series and one of the third order — rhythm of phrases. Most stable is the rhythm of the 1st order. The special case represents signal of *Lithodusa daghestanica*. Its structure can be interpeted as 3-pulsed series following one after another with very short interval, comparable with intervals between pulses. The temporary structure of repeating 3-pulsed element of the signal is very similar to those of *A. picta*: 3rd pulse (opening pulse in *Lithodusa*) has largest duration, the middle pulse has minimal duration. Besides them interval between 1st and 2nd pulses is shorter than interval between 2nd and 3rd pulses. These peculiarities of the calling song suggest an opportunity of an origin their 3-pulsed series from phrases consisting from two 2-pulsed series. As in *A. picta*, it may be a result of loss of the 1st pulse of the 1st series. Temporal pattern of *Lithodusa* song might be explained also through alternating activity of the two rhythm generators: one of them controls pulse rate in pulse sequence (trill) and the second one provides two-pulsed series rate. Other explanations of this phenomenon are possible also. Similar pattern occurs in one of part of the song of *Conocephalus discolor* [Heller, 1988; Ragge, Reynolds, 1998].

Besides songs studied in this work it is known calling signals only three mediterranean Drymadusini species: *Drymadusa dorsalis, Anadrymadusa ornatipennis* and *Paradrymadusa aksirayi* [Heller, 1988] and 7 nearctic species of *Atlanticus* [Walker, 1975; Walker, Moore, 2001]. In *Drymadusa, Anadrymadusa* and *Paradrymadusa* they are regularly repeatuing one-, three- and 11-pulsed series respectively.

North american *Atlanticus*' songs are regularly repeating as in *Phytodrymadusa* spp. short trills (*A. americanus*, *A. glaber, A. monticola*) or long trills (*A. calcaratus*). Males of *A. testaceus* produce long lasting dense sequences of two-pulsed series. Calling song of *A. gibbosus* is rhythmically repeated phrases — sequences consisting of 8–12 pairs of closing pulses. One species (*A. dorsalis)* produces sequences of one pulsed series. Thus, in the Drymadusini we can see almost all known variants of rhythmic patterns of bush cricket's signals, and we will try to present probable ways of evolution of a signal in this tribe. Their hypothetical scheme is given in Fig. 65.

The primitive song-pattern was probably a trill. The stridulation is provided with activity only of one rhythm generator (*Calopterusa pastuchovi, Atlanticus calcara-*




Figs 59–64. Power spectra of calling songs at complete cycle of tegmina movements during stridulation of *Anadrymadusa ornatipennis* (59), *A. retowskii* (60), *A. robusta* (61), *A. beckeri* (62), *Eulithoxenus mongolicus* (63), *Atlanticus brunneri* (64). Vertical scales are linear.

Рис. 59–64. Амплитудно-частотные спектры призывных сигналов при полном цикле движений надкрылий при стридуляции *Anadrymadusa ornatipennis* (59), *A. retowskii* (60), *A. robusta* (61), *A. beckeri* (62), *Eulithoxenus mongolicus* (63), *Atlanticus brunneri* (64). Вертикальная шкала в линейном масштабе.

*tus*). The addition in structure of the sound center of one more oscillator rhythmically interrupting work of the first one, results in occurrence of repeating series containing different number of pulses. The temporal pattern of a signal becomes hyerarchical — with two rhythmic levels. Such songs produce *Anadrymadusa ornatipennis, Paradrymadusa galitzini, P. aksirayi, Atlanticus brunneri, A. testaceus, Eulithoxenus mongolicus* and *Phytodrymadusa* spp. Rhythm of the second oscillator activity can be very low (several times per minute as in *Phytodrymadusa* spp.*) or very high as in *Atlanticus brunneri* (up to 10 per s). In the last case the song remindes a trill. There is also a theoretical opportunity of existence of two nonhyerarchically connected oscillators with alternating activity as was considered above for *Lithodusa.*

The next step of signal's progressive evolution is appearance of rhytmically repeated phrases — groups of series sequences. Three rhythmic levels occure in these songs: the first level — pulse repetition rate, the second one — series repetition rate and the third one — rhythm of phrases. To species with these calling signals belong *A. retowskii* and *A.robusta.* Their sound centers obviously are most complex as should include maximal number of hyerarchically organized oscillators.

The even greater variety of signals is achieved as a result of change of separate structural elements of a

*) Studied *Phytodrymadusa* spp. emit periodically repeating sequences of more than 50 or 100 pulses and such signals significantly differ from songs with fixed pulse number in short series of another bush cricket species. Probably interruptions in singing in *Phytodrymadusa* might be caused by fatigue and thus pulse sequences in these species are not series, but short trills.

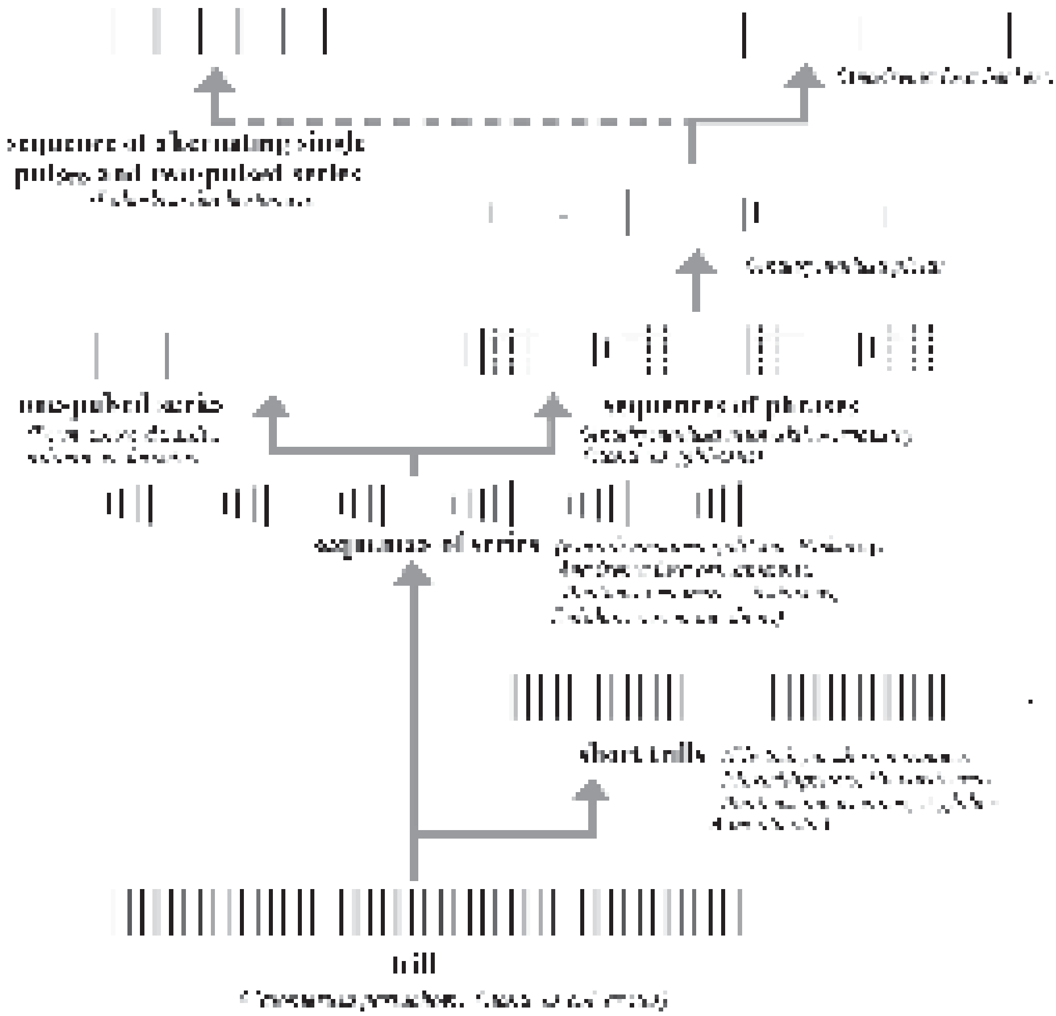



Fig. 65. Hypothetical scheme of the ways of calling signal evolution in tribe Drymadusini. It is shown the closing pulses only.
Рис. 65. Гипотетическая схема путей эволюции призывного сигнала в трибе Drymadusini. Показаны только пульсы, возникающие при закрывании надкрылий.

signal (for example, reduction of number of pulses in series), instead of as a result of complication of its hyerarchical rhytmical structure. It, apparently, occurs rather easily, since even at steadily singing males *A. robusta* and *A. picta* from time to time decrease of amplitude or loss of the first pulse in series (Figs 43, 44) are observed. Wing movement recordings show that in greek specimen of *A. ornatipennis* amplitude of muscle contraction during second pulse and sound amplitude correspondingly are lower than of other ones [Heller, 1988]. Different events can follow to this result: a change of a force of opening muscles contraction or elongation of activity 2nd and 3rd order oscillators. Thus there is observed a regressive evolution of the Drymadusini songs. It is necessary to note a parallelisms in development of rhythmic pattern of calling signals in this tribe. Similar song types occur in some North american *Atlanticus spp.* and transcaucasical endemic species of *Phytodrymadusa* — there are short trills with low but rather stable repetition rate.

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